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Dorsostable Lumbar Region in Hominoidea: Homology or Homoplasy?

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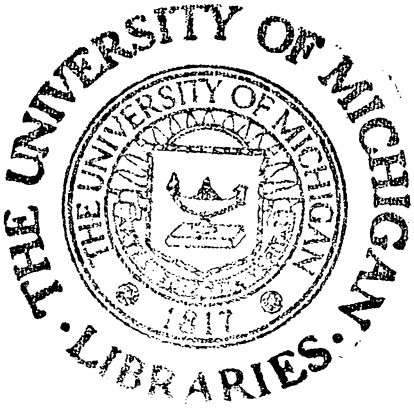
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Dorsostable Lumbar Region in Hominoidea: Homology or Homoplasy?

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Abstract

African apes (*Pan*, *Gorilla*) and orang-utans (*Pongo*) have positional repertoires that include forelimb-dominated behaviors such as climbing, bridging, below-branch suspension, and brachiation. These behaviors benefit mechanically and kinematically from dorsostability of the lumbosacral region of the spine. However, due to inconsistencies between character complexes there is continuing debate about whether skeletal adaptations underlying dorsostability are synapomorphies of the great ape clade, or homoplasious. The late Miocene ape *Sivapithecus* is interpreted as the sister taxon to *Pongo* based on craniofacial similarities, but has a primitive postcrania adapted for pronograde activities and lacking features for forelimb-dominated behaviors. Conversely, some adaptations for dorsostability of the lower spine and presumably modern-type behaviors were already present in fossil great apes (e.g. *Morotopithecus*) as early as the early Miocene. This indicates that either *Sivapithecus* is not the sister taxon to *Pongo* or the *Pongo-Sivapithecus* clade developed lumbosacral dorsostability separately from the African ape-*Morotopithecus* clade, and postcranial features shared between African apes and orang-utans arose via parallel evolution. In such case it would be expected that significant differences between African apes and orang-utans would emerge upon closer examination of the axial postcranium.

Previous analyses have concentrated on the appendicular skeleton. This study focuses on the axial postcranium, in particular the lumbosacral region, which in mammals is functionally correlated with positional capabilities. The results show that members of the African ape–*Homo* clade accomplish dorsostability via similar functional complexes, while *Pongo* accomplishes dorsostability via a unique functional complex comprising an

unusual combination of pedicle robustness, transverse process position, and prezygapophyseal angulation. These and other vertebral traits differentiate *Pongo* from African apes, indicating that dorsostability and associated behaviors independently arose multiple times in large-bodied apes.

Introduction

All extant great apes (*Pan*, *Gorilla*, *Pongo*) and humans (*Homo*) share a dorsostable or stiff back condition in the lumbosacral region that is functionally correlated with a number of forelimb-dominated behaviors. This condition was originally assumed to be a synapomorphy of all great apes, a characteristic inherited from their most recent common ancestor; discovery of more fossil material has cast doubt on this assumption. *Sivapithecus*, *Ouranopithecus*, *Dryopithecus* and *Morotopithecus* are important fossil Miocene hominoids that have helped to polarize hominoid phylogeny. Certain lumbosacral adaptations for dorsostability have been found in *Morotopithecus* (Sanders and Bodenbender, 1994; MacLatchy et al., 2000), indicating that dorsostability has either been developing since before the African ape-orang-utan split or is a convergent characteristic and has arisen multiple times independently in the evolution of large-bodied apes (Kelley, 2002). *Ouranopithecus* and *Dryopithecus* are more similar cranially and postcranially to African apes and hominids than to *Pongo* (Andrews et al., 1997), which has generally been considered the sister taxon to *Sivapithecus* based primarily on craniofacial similarities. However, *Sivapithecus* postcranial elements described by Pilbeam et al. (1990) proved to be more primitive than those of its dorsostable contemporaries, lacking features necessary for forelimb-dominated behaviors shared by extant great apes (Pilbeam et al., 1990; Larson, 1998). The glaring discrepancies between the evolutionary paths suggested by cranial versus postcranial characters indicate that one of the apparently homologous character complexes is actually homoplasious.

Three hypotheses have been proposed to account for this dichotomy of craniofacial and postcranial characteristics (e.g., Pilbeam et al., 1990; Begun and Kordos, 1997; Ward, 1997; see Figure 1). Hypothesis A states that lumbosacral dorsostability is a primitive characteristic of large-bodied hominoids, emerging at least by the Lower Miocene, as demonstrated by the dorsostable vertebral morphology of *Morotopithecus*, and that postcranial similarities among extant great apes are homologies. The craniofacial similarities between *Sivapithecus* and *Pongo* are considered homologous, and the pronograde-adapted postcrania of *Sivapithecus* a reversal from the primitive dorsostable and forelimb-dominated condition. However, *Sivapithecus* postcrania are very similar to those of contemporary non-dorsostable hominoids, rendering such a reversal unlikely. Hypothesis B also considers lumbosacral dorsostability to be a primitive homologous trait among extant great apes, but craniofacial similarities between *Sivapithecus* and *Pongo* are homoplasies and the two are not sister taxa. Hypothesis C considers *Sivapithecus-Pongo* craniofacial similarities homologous and identifies lumbosacral dorsostability and postcranial similarities among extant great apes as homoplasious characteristics that arose multiple times among the great apes. This hypothesis would predict lumbosacral morphological differences between *Pongo* and the African ape-*Homo* clade to emerge under closer examination.

Previous studies of hominoid postcrania have examined characters associated with forelimb-dominated behaviors, concentrating on the appendicular rather than axial skeleton (e.g., McCrossin and Benefit, 1997; Rose, 1997; Larson, 1998). This study compares the axial morphological complexes that are associated with lumbosacral dorsostability in extant great apes. A high degree of similarity between African apes and the orang-utan would support Hypothesis A or B (this study could not distinguish between these hypotheses because only extant hominoids were included in the analysis). Conversely, significant morphological differences would support Hypothesis C, indicating the independent acquisition of dorsostability in *Pongo* and the African ape-*Homo* clade.

Materials & Methods

Three extant great apes (*Pongo pygmaeus*, *Pan troglodytes troglodytes*, and *Gorilla gorilla gorilla*), humans (*Homo sapiens*) and *Hylobates* spp. were examined in an attempt to determine the homologous or homoplasious nature of lumbosacral dorsostability in extant great apes. All vertebral measurements were taken directly from Sanders (1995). Nine measurements of each of the four caudal-most lumbars and one measurement of the cranial-most sacral vertebra were analyzed (see Figure 2), as well as the numbers of vertebrae in each region of the column and live body weight, and were used to discern morphological differences correlated with lumbosacral dorsostability between extant hominoids. Seven of the nine vertebral measurements were taken using digital calipers accurate to +/- 0.02mm, while two (prezygapophyseal angle and the distance from the transverse process to the junction of pedicle and vertebral body) were measured using the computer graphics program Optimus from scaled photographs (all measurements used are from Sanders, 1995). Body weights were taken from Smith and Jungers (1997). See Table 1 and Figure 2 for measurement descriptions. Linear measurements and body weights were natural log transformed to compensate for biological variability (Gingerich, 2000). Species were divided by sex to avoid bias due to the varying degrees of sexual dimorphism present in hominoids. Cercopithecoidea was used as a non-dorsostable outgroup to help determine character polarity within the great-ape clade.

Mean natural log-transformed measurements for males and females of each taxon (*Homo*, *Pongo*, *Gorilla*, *Pan*, and one hylobatid) were compiled and analyzed using principal components analysis. Multivariate analyses require all entries to contain the same number of data points, so any specimens or species for which some data were missing were excluded. The number of specimens used from each group is listed in Table 3. The number of lumbar vertebrae in these species range from 4 to 7. Sanders (1995) declares that based on the branching patterns of lumbar spinal nerves and columnar force transmission anterior lumbars have been lost, suggesting that the last four lumbars are equivalent even between species with varying numbers of lumbars. Since this study focused on the dorsostability of the lumbosacral region, only data for the posterior four

lumbars and the first sacral vertebrae were included in the principal components analysis. In the figures illustrating the measurements that had a significant impact on the distribution along the principal component axes all vertebrae and all species are included, although some of these were not included in the principal components analysis either because data was incomplete or the inclusion of an outgroup skewed the principal components analysis. For example, Cercopithecoids were excluded from the principal components analysis because their inclusion altered the principal component loadings, obscuring relationships between extant large-bodied hominoids, the subject of this study.

Results

The results of a principal components analysis of vertebral measurements of 4 species of extant great apes and *Hylobates* spp. are shown graphically in Figure 3. Numerical scores for the principal components are listed in Table 2.

PC-I The first principal component separates extant hominoids along an axis spanning about 7.4 ln unit, with the greatest dispersal between hylobatids and great apes. Inclusion of hylobatids did not significantly alter the variables described by the principal components and were included as an indicator of outgroup morphology. PC-I has an eigenvalue of 6.059, corresponding to 80.6% of the total variance in the measurements. PC-I primarily describes size, with high positive eigenvector coefficients or loadings for variables such as measurements of the vertebral body, body weight, pedicle robustness, transverse process position, and neural spine length, and high negative loadings for prezygapophyseal characteristics of the upper lumbars.

PC-II The second principal component separates hominoids along an orthogonal axis spanning about 2.4 ln units, separating *Pongo* and *Homo* from the African apes. PC-II has an eigenvalue of 0.863, corresponding to 11.5% of the total variance in the measurements. The position of the diaphragmatic vertebra, and the number of thoracic and sacral vertebrae had high positive loadings, while the prezygapophyseal angle and

vertebral body shape of the last lumbar and first sacral vertebra and the number of lumbar vertebrae had high negative loadings.

PC-III The third principal component spans an orthogonal axis of about 1.7 ln units, separating *Pongo* from all other hominoids included in the analysis. PC-III has an eigenvalue of 0.347, corresponding to 4.6% of the total variance. This separation primarily occurs based on the number of lumbar vertebrae (positive loading) and prezygapophyseal angles of the 5^{th} and 6^{th} lumbar vertebrae (negative loadings).

PC-IV The fourth principal component spans an orthogonal axis of about 1.3 ln units, separating *Pan* and *Gorilla* from each other and from all other hominoids included in the analysis. PC-IV has an eigenvalue of 0.179, corresponding to 2.4% of the total variance. This separation is based on the number of sacral vertebrae (high positive loading) and prezygapophysesal angles of the posterior lumbars (negative loading).

- Pedicle Breadth -

Pedicle breadth is one of the important variables in separation along PC-I. Pedicle robustness is highly correlated with overall body size and is closely related to force dispersal (see discussion). The great body weight of the male *Gorilla* results in force dispersal requirements that rival those necessitated by habitual bipedality in *Homo* (see Figure 4). Pedicle breadth increases in the last one or more lumbar vertebrae in all hominoids and cercopithecoids except *Pongo*, where it decreases in the caudal-most lumbar. This will be examined further in the discussion section.

- Transverse Process Location -

Transverse processes arise off of the pedicle of each lumbar vertebra in all large-bodied hominoids. In African apes and *Homo* the processes are located in consecutively more ventral positions in the more posterior lumbars (see Figure 5). Conversely, the transverse process on the last lumbar in *Pongo* is positioned more dorsally than on anterior lumbars. The transverse processes of hylobatids and cercepithecoids are also positioned more dorsally on the posterior lumbar vertebrae than on anterior lumbars. However, the

processes arise off of the vertebral body rather than the pedicle as in large-bodied hominoids and only in the last lumbar vertebra of hylobatids do the processes migrate up onto the pedicle. The similarity between *Pongo* and the outgroups is thus superficial, and the more dorsal position of the process on the last lumbar is not a primitive characteristic and is instead an autapomorphy of *Pongo,* while the more ventral positioning seen in African apes and *Homo* is a homologous characteristic within that clade.

- Prezygapophyseal Angle -

The primitive condition of this character as typified by cercopithecoids is a relatively consistent prezygapophyseal angle throughout the lumbosacral column. See Figure 6. *Gorilla*, *Pan* and hylobatids display a significant decrease in prezygapophyseal angle between the last lumbar and first sacral vertebra. Conversely, *Pongo* demonstrates consistent incremental changes in prezygapophyseal angle from the first lumbar through the first sacral vertebra. This is similar to the highly derived condition seen in *Homo*, where it is functionally related to bipedality.

- Number of Vertebrae -

Sacral: All hominoids have 5 sacral vertebrae except for *Pan,* which has 6. This is the most significant characteristic in PC-IV, the principal component that separates *Pan* and *Gorilla.*

Lumbar: The number of lumbars have been reduced from the primitive 7 seen in cercopithecoids to 5 in hylobatids, and further reduced to only 4 in all large-bodied hominoids except *Homo,* which has secondarily altered the last thoracic into a lumbar, resulting in one fewer thoracic and one extra lumbar compared with African apes.

Thoracic: The orang-utan *Pongo* has 12 thoracics, while all other large-bodied hominoids except *Homo* have 13 or more. As stated above, *Homo* is highly derived within the African ape-hominid clade and has secondarily altered the last thoracic into a lumbar, as stated above. *Pongo*, however, has actually reduced the total number of vertebrae. This similarity is hence seen to be superficial and homoplasious between

Homo and *Pongo* rather than being an indicator of homologous lumbosacral dorsostability among extant large bodied hominoids.

Discussion

The principal components analysis of the relative vertebral proportions detailed above demonstrates significant differences between *Pongo* and African apes, indicating a unique functional complex in *Pongo* that is correlated with a form of lumbosacral dorsostability similar to that of African apes and *Homo*. *Homo* is highly derived relative to African apes and has a number of unusual lumbosacral characteristics that have evolved to permit habitual bipedality. In all extant great apes ligaments run from the iliac crest of the pelvis to the transverse processes of the last lumbar vertebra. The transverse processes are positioned more ventrally on the pedicle of this lumbar than on preceding vertebrae in African apes and hominids. This places the iliac ligament in a more efficient orientation, acting sub-parallel rather than perpendicular to forces and reducing much of the force on the lumbo-sacral articulation. Since the ligaments are placing stress on the transverse processes, which are situated on the pedicle in large-bodied hominoids, the pedicle breadth in posterior lumbars of African apes and *Homo* is increased to help absorb the stress. The drastic increase in pedicle breadth (as well as transverse process robustness and decrease in transverse process length) in the last lumbar of *Homo*, as opposed to the lesser increase seen in African apes, is correlated with the greater force-dispersal requirements of habitual bipedality. As noted above, *Pongo* narrows the pedicle and raises the transverse processes of the last lumbar vertebra, which would appear to reduce dorsostabilty in the lumbosacral region (figure 4).

Additional force is dispersed through wide, flat prezygapophyses of the last lumbar and first sacral in *Homo*, which help prevent slippage of the last lumbar vertebra in conjunction with lumbar lordosis associated with habitual bipedality. *Pongo* has similar prezygapophyseal morphology, though no lumbar lordosis, permitting considerable rotational motion but little in the sagittal plane. The prezygapophyseal angle of the first

sacral steepens in African apes and the two outgoups, reducing the torsional mobility of the lumbosacral region (figure 6).

Extant great apes display two distinct morphological complexes that are correlated with varying levels of force dispersal requirements and lumbosacral dorsostability. One is an iliac ligamentous complex related to increased pedicle robustness and more ventrally positioned transverse processes on the caudal-most lumbar. The other is defined by increased prezygapophyseal angulation and a reduced number of thoracic vertebrae. The first morphological complex is present in African apes, and is even more pronounced in *Homo*. The unusual dedicated behavior of *Homo*, habitual bipedality, is dependent on specialized vertebral morphology to disperse the larger forces and prevent misalignment of lower lumbars and the vertebral column on the sacrum, dangers which increase with pelvic rotation and lumbar lordosis. (Lumbar lordosis, a condition in which the vertebral column is ventrally convex, is unique to humans among catarrhine primates. This ventral convexity is directly associated with bipedality.) The first morphological complex appears to be a synapomorphy of the African ape-hominid clade, while hominids integrated an increased prezygapophyseal angulation into the existing complex to compensate for the increased stresses incurred by habitual bipedality and lumbar lordosis. Like *Homo*, *Pongo* increases the prezygapophyseal angulation in posterior lumbars, indicating that increased prezygapophyseal angulation in the posterior lumbars is actually a homoplasious condition for increasing lumbosacral dorsostability among large-bodied hominoids.

The accepted phylogeny of extant great apes is quite stable, although there is a large amount of dissention concerning where fossil hominoids should be placed (e.g. Pilbeam et al., 1990; Begun and Kordos, 1997; Ward, 1997). The question being addressed here is simply, where do the morphological characters correlated with lumbosacral dorsostability map onto the accepted phylogenetic tree and what evolutionary conclusions can be drawn from the pattern.

Because one morphological complex is restricted to one branch of the phylogenetic tree (African apes and hominids) and the other complex is shared between the most derived member of that branch (*Homo*) and the sole extant representative of a separate branch (*Pongo*) it is most probable that neither morphological complex correlated with lumbosacral dorsostability developed before the African ape-*Pongo* split. Lumbosacral dorsostability appears to be a homoplasious condition in extant large bodied hominoids, arising separately in different branches of Hominoidea via differing morphological complexes.

Conclusion

The morphological complex associated with a degree of dorsostability in all extant hominoids is associated with fewer lumbar vertebrae, loss of anticliny, movement of the transverse processes onto the pedicles from the vertebral bodies, and shortening of lumbar vertebral bodies. However, extant great apes require a greater degree of lumbosacral dorsostability than the amount adequate for the much smaller hylobatids. In extant large-bodied hominoids dorsostability has been increased via two different additional morphological complexes, one of which is synapomorphic and one of which is homoplasious.

Dorsostability in African apes emerged as a functional correlate of a morphological complex comprising increased pedicle robustness and transverse processes positioned ventrally on the caudal-most lumbar. *Pongo* has an unusual combination of lumbosacral pedicle robustness, transverse process position, and prezygapophyseal angulation, all of which are primitive, autapomorphic, or homoplasious characters. As such, none are individually useful for determining phylogenetic relationships. However, these vertebral measurements together comprise a morphologically unique functional complex correlated with lumbosacral dorsostability in *Pongo* that is functionally similar to that present in African apes and *Homo*.

The increased functional requirements that emerged with habitual bipedalism in *Homo* were met by the incorporation of increased prezygapophseal angulation in the posterior lumbars and anterior sacral, similar to that identified in *Pongo* but acquired independently, into the inherited African ape dorsostable complex, combining to provide a greater degree of dorsostability and vertebral force dispersal. These findings support the phylogenetic affinities outlined in Hypothesis C, with *Sivapithecus* as the sister taxon to *Pongo* and the Lower Miocene hominoids which demonstrate lumbosacral dorsostability more closely related to African apes than to *Pongo*, and indicate that lumbosacral dorsostability and associated behaviors arose independently multiple times via differing vertebral morphologies in the evolution of large-bodied hominoids.

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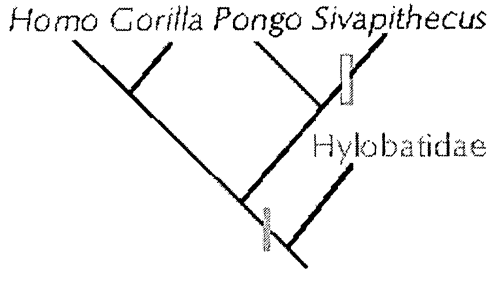
Figure 1: Three hypotheses have been proposed concerning the homologous or homoplasious states of postcranial vs. craniofacial character complexes and whether lumbosacral dorsostability is a primitive or homoplasious characteristic of extant large bodied hominoids. These cladograms illustrate the hypotheses: grey bars indicate the acquisition of dorsostability; the white bar indicates secondary loss.

Hypothesis A: Lumbosacral dorsostability is a primitive characteristic of extant large bodied hominoids; *Sivapithecus* and *Pongo* are sister taxa, and *Sivapithecus* secondarily lost lumbosacral dorsostability.

Hypothesis B: Lumbosacral dorsostability is a primitive characteristic of extant large bodied hominoids; *Sivapithecus* and *Pongo* are not sister taxa.

Hypothesis C: Lumbosacral dorsostability is a homoplasious characteristic of extant large bodied hominoids, arising separately in *Pongo* and the African ape-hominid clade; *Sivapithecus* and *Pongo* are sister taxa.



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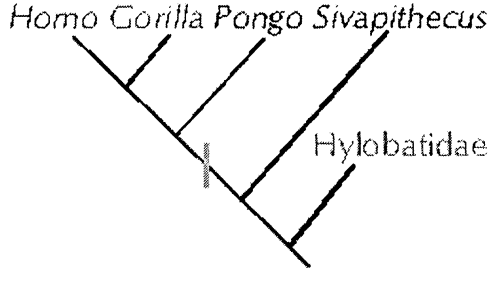

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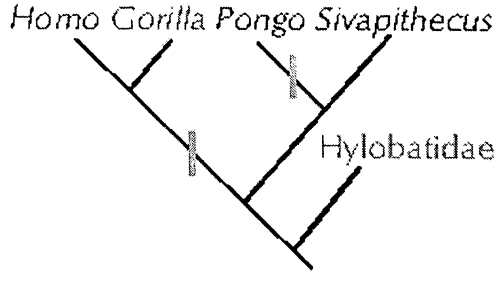


Hypothesis C

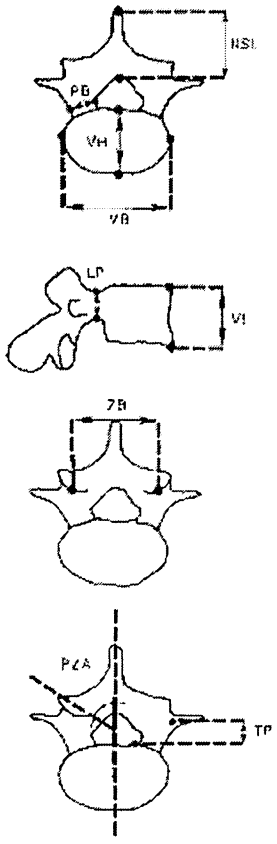


Figure 2: Measurements used in study, described in Table 1. After Sanders, 1995.

Table 1: Vertebral measurements used in this study, illustrated in Figure 2. Linear measurements are in mm; angles in degrees. After Sanders, 1995.

Abrev	Measurement	Description
VB	Vertebral body breadth, cranial	Greatest width, cranial end of centrum
VH	Vertebral body height, cranial	Height of centrum, cranial end, measured in the midline sagittal plane
VL	Vertebral body length, ventral	Length of centrum along the ventral margin
PB	Pedicle breadth	Minimum transverse diameter of the pedicle, usually on the right side
LP	Pedicle length	Minimum length of the pedicle, usually on the right side
NSL	Neural spine length	Length of the neural spine from the dorsalmost margin of the vertebral foramen to the apex of the neural spine
PZA[1]	Prezygapophyseal angle	Angle formed by a straight line along the medial and lateral edges of a prezygapophyseal facet, right side, as it intersects a midline sagittal line through the centrum
ZB	Prezygapophyseal breadth	Distance between the midpoints of right and left prezygapophyseal facets
TP[1, 2]	Transverse process	Distance between the center of the transverse process root and the dorsal vertebral body margin – signed to indicate dorsal or ventral of the margin
TPL[2]	Transverse process position index	TP*100 / VH An index describing TP relative to VH; positive numbers indicate that the transverse process root is ventral to the dorsal margin of the centrum, and negative numbers indicate that the root is dorsal to the dorsal margin of the vertebral body
TPH	Transverse process height	TP+VH Unsigned description of transverse process position
VBS	Vertebral body shape	VB*100 / VL An index describing VB relative to VL; values > 100 describe centra wider than long, and values < 100 describe centra longer than wide

[1] Measurements calculated by image analysis of scaled photographs.
[2] Measurements not included in principal components analysis.

Table 2: Numerical scores (Eigenvectors) for the principal components analysis. Variable abbreviations are defined in Table 1.

Variable	PC 1	PC 2	PC 3	PC 4
Body Weight	0.448	0.083	-0.228	-0.066
#Thoracic Vertebrae	-0.068	0.495	0.265	-0.117
#Lumbar Vertebrae	-0.104	-0.329	0.539	-0.110
#Sacral Vertebrae	0.018	0.254	0.051	0.812
Diaphragmatic Vertebra	-0.033	0.566	0.101	-0.317
VB – L4	0.141	-0.045	0.016	-0.042
VB – L5	0.144	-0.048	0.019	-0.018
VB – L6	0.148	-0.049	0.024	-0.025
VB – L7	0.148	-0.054	0.011	-0.037
VH – L4	0.160	-0.034	-0.029	0.047
VH – L5	0.158	-0.037	-0.032	0.081
VH – L6	0.159	-0.041	-0.047	0.102
VH – L7	0.159	-0.056	-0.013	0.122
VL – L4	0.120	-0.037	-0.020	-0.084
VL – L5	0.115	-0.031	0.012	-0.049
VL – L6	0.124	-0.031	-0.020	-0.029
VL – L7	0.137	-0.024	-0.030	-0.023
PB – L4	0.206	0.012	-0.185	-0.045
PB – L5	0.203	-0.043	-0.116	0.056
PB – L6	0.212	-0.065	-0.065	-0.075
PB – L7	0.161	-0.117	0.273	-0.182
LP – L4	0.097	0.025	-0.073	-0.045
LP – L5	0.102	0.035	-0.097	-0.025
LP – L6	0.101	0.041	-0.116	-0.045
LP – L7	0.120	0.048	-0.112	0.011
NSL – L4	0.214	0.114	0.218	0.034
NSL – L5	0.204	0.098	0.220	-0.019
NSL – L6	0.205	0.123	0.175	0.010
NSL – L7	0.185	0.176	0.116	-0.061
PZA – L4	-0.077	0.080	-0.120	-0.038
PZA – L5	-0.054	0.105	-0.177	-0.133
PZA – L6	-0.038	0.008	-0.148	-0.131
PZA – L7	-0.019	-0.105	-0.072	-0.174
PZA – S	-0.006	-0.257	-0.113	-0.074
ZB – L4	0.135	0.039	0.024	-0.052
ZB – L5	0.141	0.060	0.080	-0.005
ZB – L6	0.148	0.018	0.132	-0.007
ZB – L7	0.151	-0.075	0.189	0.025
ZB – S	0.146	-0.174	0.295	0.089
TPH – L4	0.101	0.037	-0.051	-0.111
TPH – L5	0.104	0.008	-0.100	-0.032
TPH – L6	0.115	-0.023	-0.073	0.016
TPH – L7	0.149	-0.032	0.068	0.083
VBS – L4	0.021	-0.008	0.036	0.042
VBS – L5	0.030	-0.017	0.007	0.031
VBS – L6	0.024	-0.018	0.044	0.004
VBS – L7	0.011	-0.030	0.040	-0.014

Table 3: Number of specimens used to calculate mean values for each group included in the principal components analysis.

Species	**Females**	**Males**
Homo sapiens	20	20
Pan troglodytes troglodytes	13	13
Gorilla gorilla gorilla	13	20
Pongo pygmaeus	9	10
Hylobates spp	22 (6 species)	23 (7 species)

Figure 3: Principal components analysis – PC I, II, III and IV correspond to 80.5%, 11.5%, 4.6% and 2.4% of the variance respectively, accounting for 99.0% of the total variance.

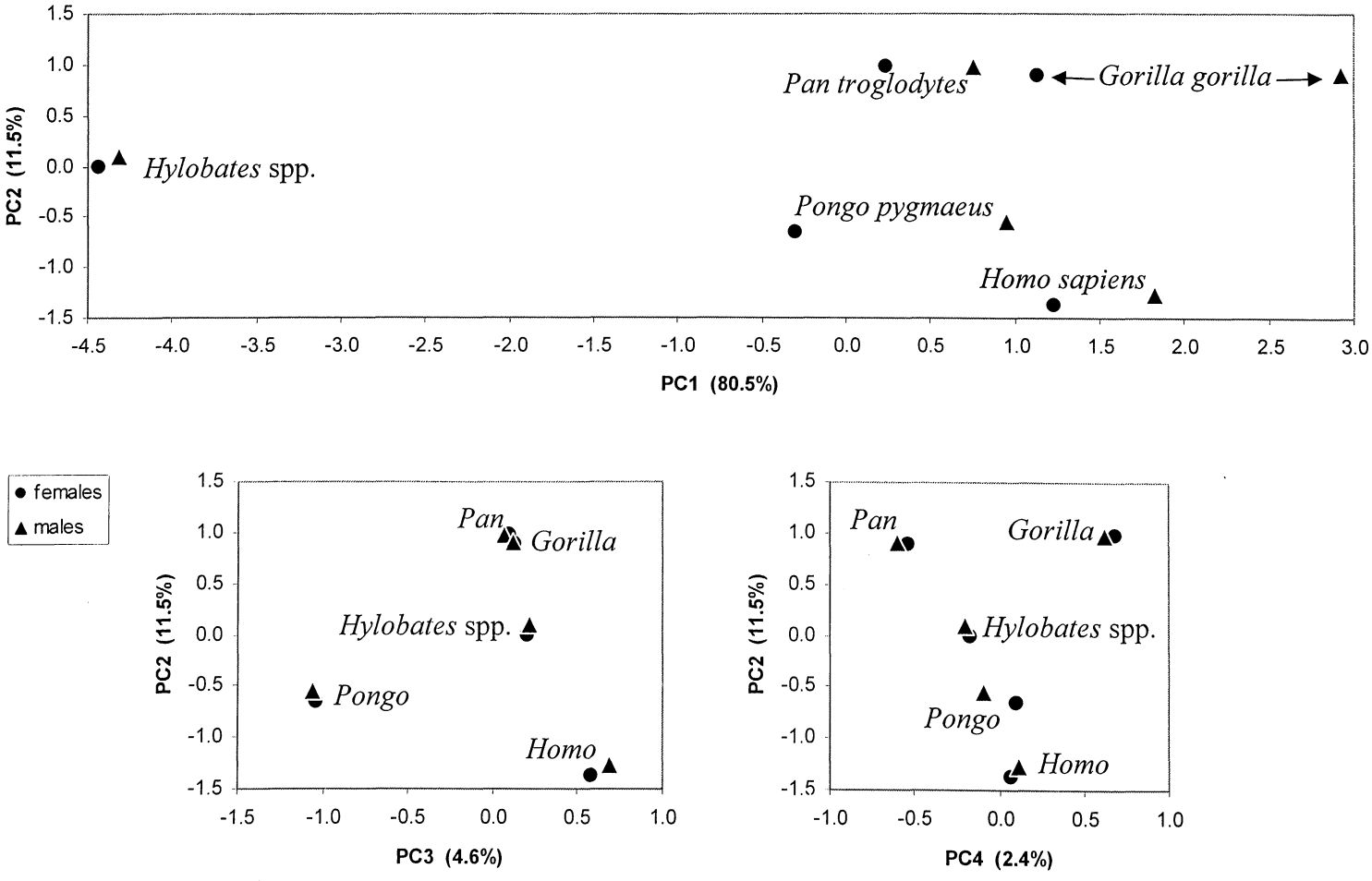


Figure 4: Pedicle Breadth – Minimum transverse diameter of the pedicle. Notice that pedicle breadth increases in the posterior lumbar vertebrae in all species except *Pongo*, in which pedicle breadth decreases in the last lumbar vertebra.

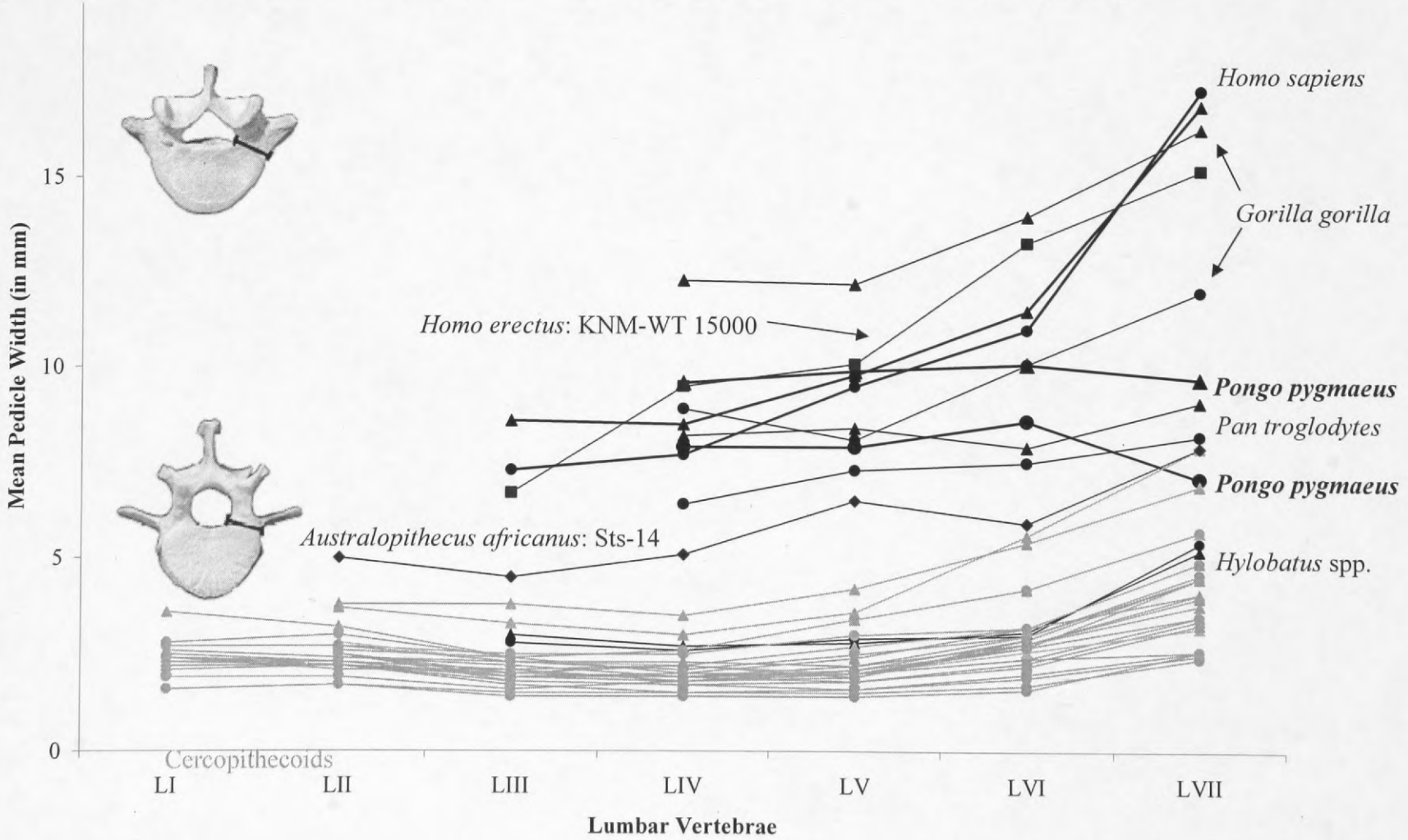


Figure 5: Transverse Process Position - An index describing distance of the transverse process from the junction of the vertebral body and the pedicle relative to vertebral body height. Positive values indicate processes arise off the vertebral body and negative values off the pedicle. The y-axis has been inverted in this figure.

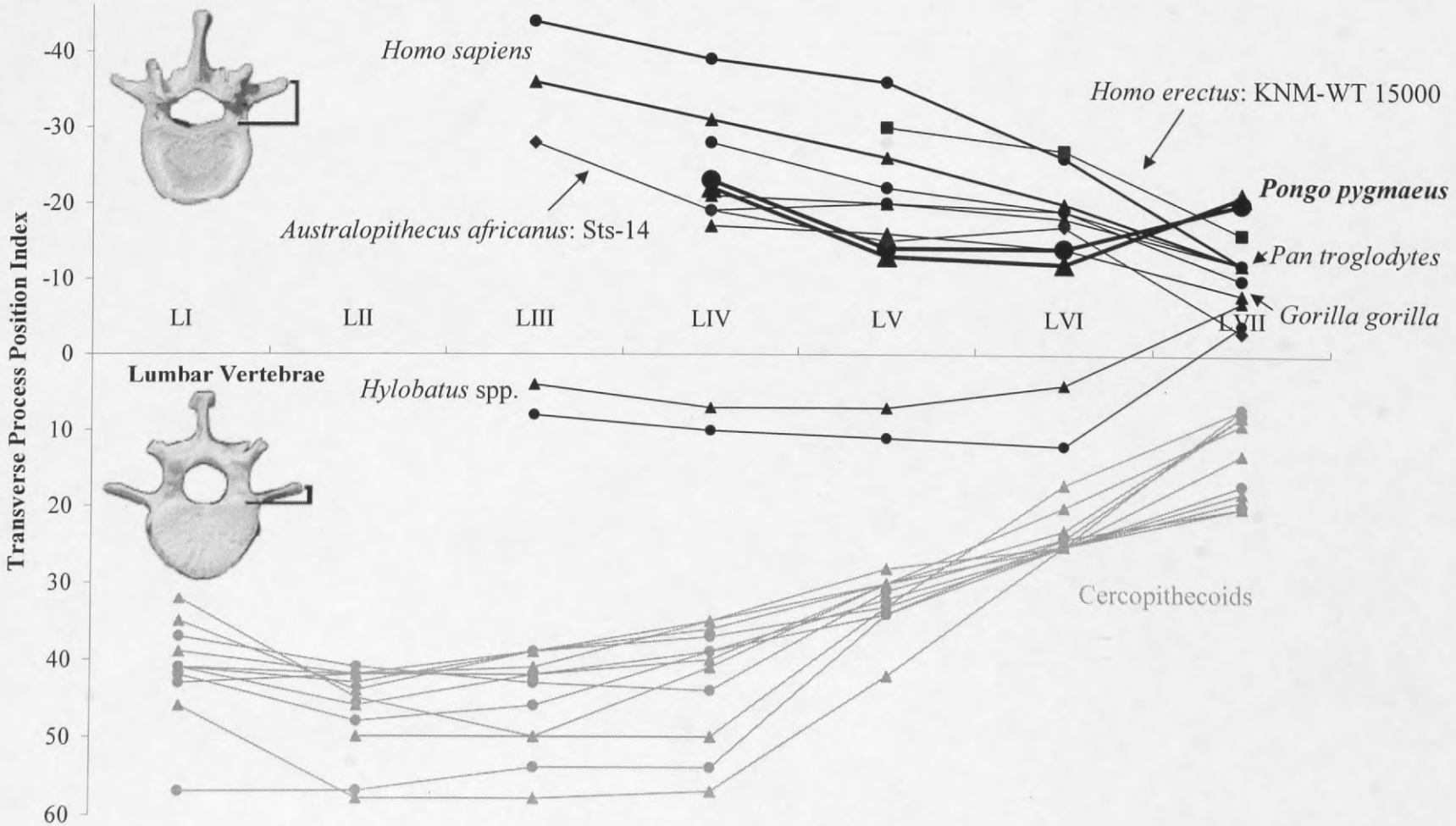
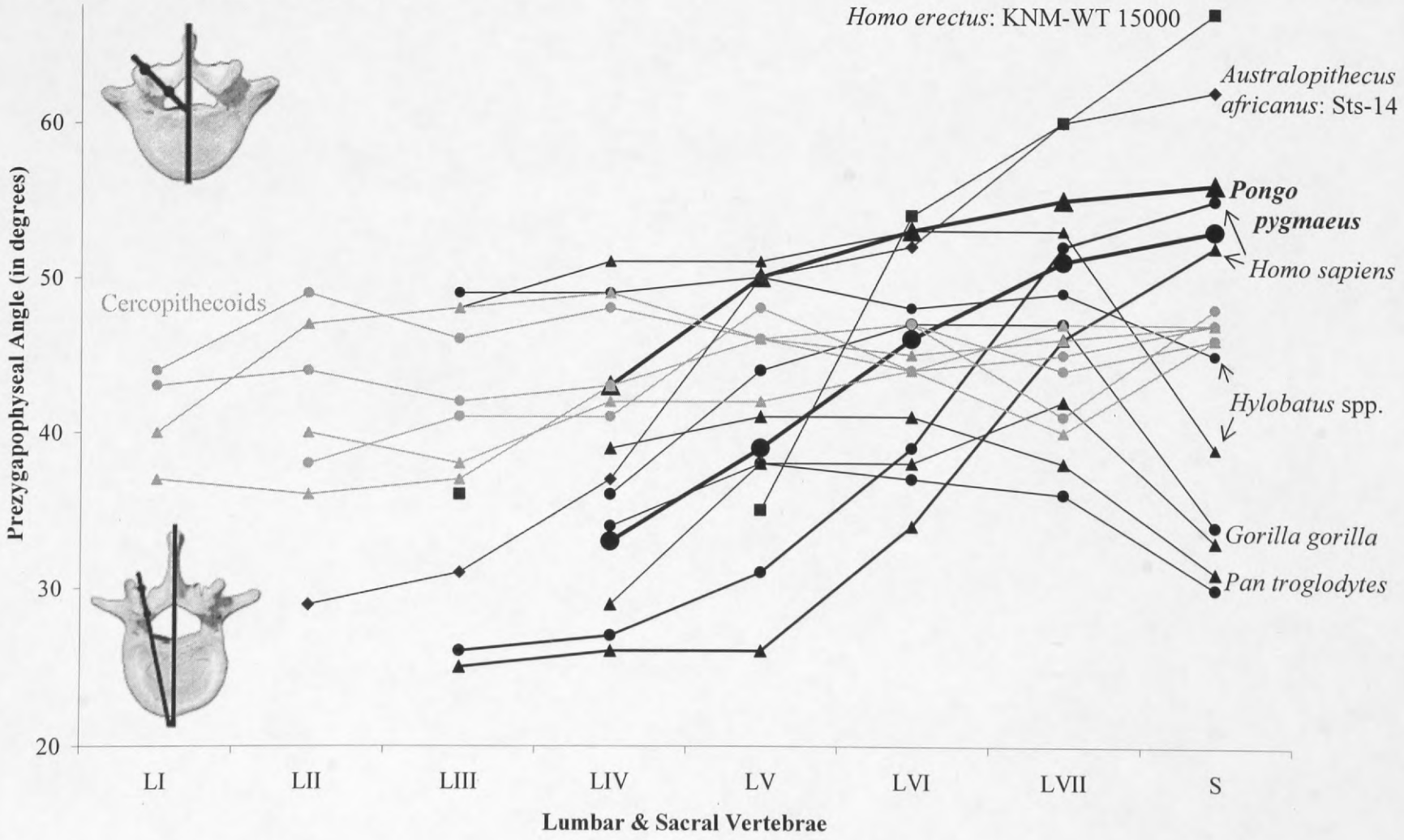


Figure 6: Prezygapophyseal Angle - Angle between the sagittal line through the vertebral body and the line along the medial and lateral edges of the right prezygapophyseal facet.



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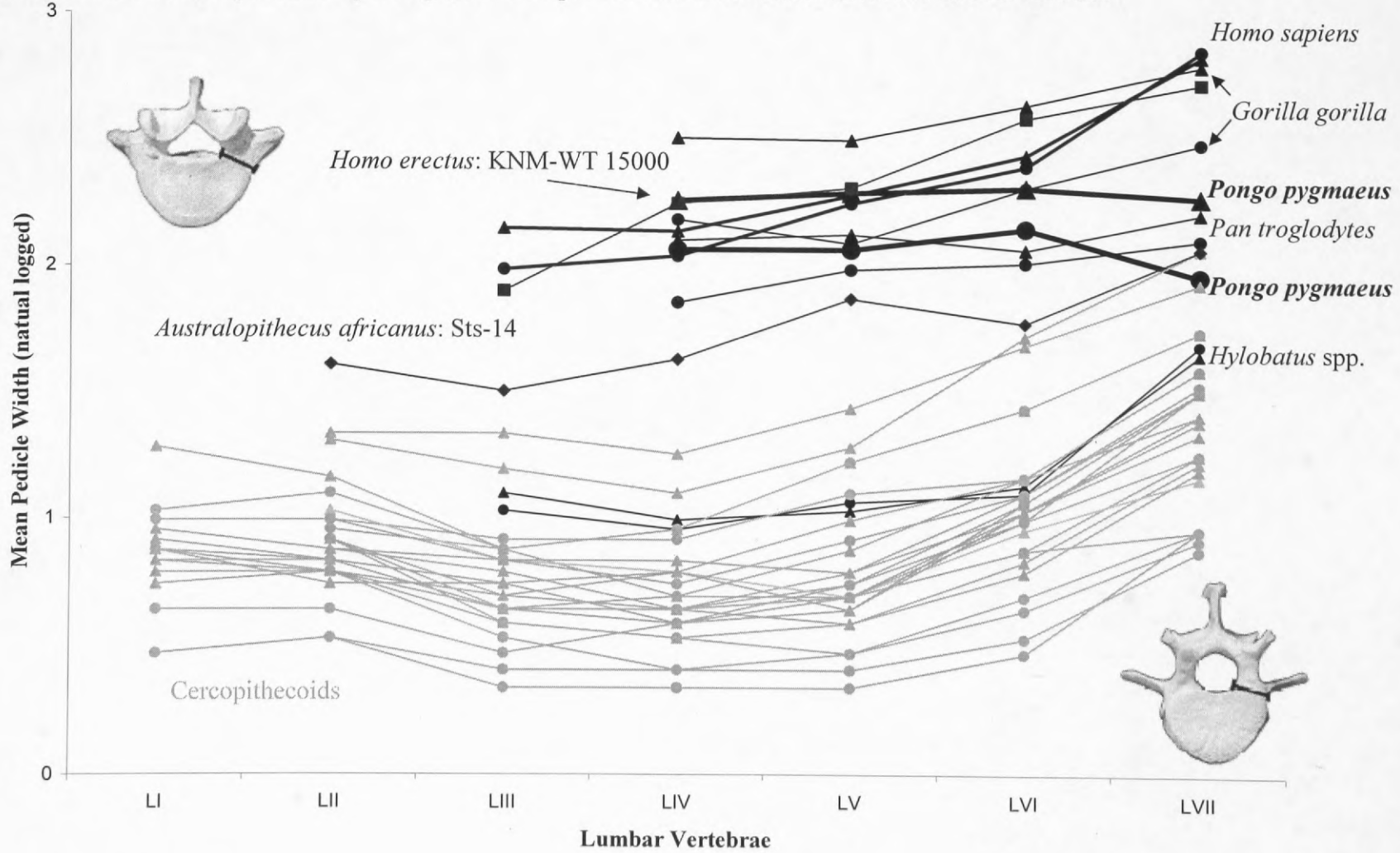

Figure 6: Prezygapophyseal Angle - Angle between the sagittal line through the vertebral body and the line along the medial and lateral edges of the right prezygapophyseal facet.